Chapter 15

Alternative reproductive tactics in primates

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A wide diversity of reproductive strategies and alternative reproductive tactics (ARTs) have evolved to promote the reproductive success of individual male and female primates. Intraspecific variation in male mating strategies has received far more attention than flexibility of reproductive behavior in female primates. However, female primates may also employ ARTs, with important implications for lifetime reproductive success. ARTs in primates tend to be limited to behavior, gonads, and physiology and are rarely associated with dramatic alternative morphologies, although striking exceptions to this rule exist. This is likely due to the advantages of plasticity and the lower costs of adjustment according to changing characteristics of the individual and social conditions. Most ARTs in primates appear to be "best-of–a-bad- job" phenotypes, whereby inferior individuals, or those in a suboptimal situation, make the most of any opportunity available to gain reproductive success. With the exception of female reproductive suppression in common marmosets, relatively little is known about the life-history pathways underlying ARTs and the factors that determine their expression. Finally, male and female reproductive strategies are intricately linked in primates, and interactions between the sexes play an important role in the evolution of primate ARTs.

15.1 Introduction

The adaptive adjustment of individuals to differences in their social and ecological environment is expected to lead to intraspecific variation in reproductive tactics (Rubenstein 1980, Dunbar 1982, Clutton-Brock 1989, Davies 1991, Lott 1991). Where consistent and discrete variation occurs in the reproductive behavior of one sex within a population, and the

tactics serve the same functional end, they are referred to as alternative reproductive tactics (ARTs) (Brockman *et al.* 1979, Rubenstein 1980, Dominey 1984). ARTs have been demonstrated for a variety of taxa, including insects, Crustacea, fish, amphibians, reptiles, birds, and mammals (chapters in this volume, Henson & Warner 1997, Brockmann 2001, Schuster & Wade 2003). Alternative behavioral tactics may occur with no associated morphological differences, but often co-occur with specific morphological, physiological, and life-history differences. For example, "resident" male ruffs (*Philomachus pugnax*) have dark plumage and defend courts on a lek; "satellite" males are white and share courts with resident males (van Rhijn 1973). Similarly big-horned adult male scarab beetles (*Onthophagus* spp.) fight for access to females and males with no or tiny horns mate sneakily (Cooke 1990, Emlen 1994).

Studies of primates can contribute to our general understanding of the evolution of mating systems, reproductive strategies, and ARTs for several reasons. First, primates exhibit complex social behavior that is likely to be reflected in their reproductive tactics (Kappeler & van Schaik 2002, Setchell & Kappeler 2004). Second, primates exhibit a diversity of ecological (Sussman 1999, 2000, in press) and life-history strategies (Kappeler & Pereira 2003), as well as a variety of social organizations, social structures, and mating systems that is rivaled by few other mammalian orders (Kappeler & van Schaik 2002). We may therefore expect equally diverse reproductive strategies and tactics (Setchell & Kappeler 2003). Finally, a great deal of detailed knowledge exists concerning primate behavior and ecology in comparison to other mammals (Smuts *et al.* 1987, Lee 1999, Kappeler 2000b, Kappeler & Pereira 2003), making the order a rich source of comparative data for the investigation of mammalian reproductive strategies.

In this chapter I review the current state of knowledge of ARTs in primates. I begin with a brief introduction to ARTs, before examining types and patterns of variability in

reproductive tactics employed by individual male and female primates, and the circumstances under which alternatives have evolved. I then examine briefly the role that interactions between the sexes plays in the expression and evolution of reproductive strategies and end with some general conclusions regarding the study of ART in primates.

15.2. Assessing ARTs

ARTs can be viewed as representing strategies for the allocation of time and/or resources to different activities to maximize individual fitness (Brockmann 2001). A complete understanding of ARTs therefore requires an integrated investigative approach combining patterns of expression, behavior, morphology, development, physiology, life-history pathways, relative fitness payoffs, and the genetic basis of alternative phenotypes (Brockmann 2001). However, such knowledge is available for relatively few taxa (Henson & Warner 1997).

Taborsky (1998) has suggested that the evolution and maintenance of ARTs in a population can be assessed at three separate levels: determination, plasticity, and selection. Determination refers to whether reproductive phenotypes are genetically or environmentally determined (West-Eberhard 1979). Genetically based phenotypes are fixed, meaning that an individual can only display the phenotype determined by its genes, as in swordtails (*Xiphophorus nigrensis* and *X. pygmaeus*, Ryan & Causey 1989), ruffs (*Philomachus pugnax*, Lank *et al.* 1995), and the marine isopod *Paracerceis sculpta* (Schuster & Wade 1991). By contrast, where phenotypes are environmentally determined (facultative), each individual has the potential to display more than one phenotype. However, Taborsky (1998) and several other authors have pointed out that the distinction between genetic and environmental determination represents an artificial dichotomy, and that conditions (environmental, social,

and individual) are likely to affect the expression of all ARTs (West-Eberhard 1979, Caro & Bateson 1986, Gross 1996, Brockmann 2001).

Plasticity refers to the underlying mechanisms that regulate alternative phenotypes (Taborsky 1998). Reproductive phenotypes may be fixed for life over an individual's lifetime (irreversible), or have the potential to change over lifetime (reversible). Reversible phenotypes can be simultaneous, where an individual is able to change back and forth between different phenotypes, or sequential, where a one-time switch exists (Caro & Bateson 1986, Gross 1996, Brockmann 2001). Moore (1991) has proposed differing proximate hormonal influences for developmentally fixed and plastic phenotypes. In irreversible cases, hormones play an organizational role prior to adulthood, but hormonal levels do not vary among adult phenotypes. In reversible phenotypes, however, hormones play an activational role during adulthood, and variation occurs in hormonal characters between adult phenotypes (Moore 1991). The relative costs and benefits of ARTs for an individual change as a function of age, relative size, body condition, future reproductive opportunity, the intensity of intra-sexual competition, and prior residence or environmental conditions such as predation risk (Taborsky 1998).

Finally, ARTs can be assessed in terms of why and how selection favors more than one tactic, and why variants are maintained in a population (Taborsky 1998). ARTs have traditionally been viewed as being maintained via frequency-dependent selection (Rubenstein 1980, Hutchings & Myers 1994, Gross 1996), or by differences in the quality of individuals (Dawkins 1980, Davies 1982, Dunbar 1982, Hazel *et al.* 1990). In the former situation, the relative fitnesses of different ARTs depend on their frequency in the population, resulting in a stable mixture of phenotypes (evolutionarily stable strategy, ESS, Maynard Smith 1982). In the latter, the fitness benefits of different ARTs need not be equal and the relative costs and benefits of ARTs differ between individuals due to differences in status, such as ontogenetic

stage, age, body condition, and experience (Gross 1996). Lower quality individuals maximize their lifetime reproductive success by adopting alternative tactics and making the "best of a bad job" (Dawkins 1980, Davies 1982, Dunbar 1982), rather than by attempting to monopolize access to females, even if the ARTs employed do not provide similar fitness payoffs. Similarly, young, competitively inferior males may employ opportunistic "side-payment tactics" (Dunbar 1982), making the best of their current situation while investing in growth at the expense of high immediate levels of reproduction. ARTs thus represent an optimal response to the particular situation in which an individual finds itself.

Brockmann (2001) has shown that two (or more) ARTs are maintained in a population where the fitness curves cross, and that the factor most likely to cause this to occur is a switch in behavior based on the relationship between fitness and individual status (status-dependent selection, Gross 1996). Frequency-dependent selection thus may play a role in all ARTs, including those that are condition dependent and maintained with the ESS switch point determining the condition at which an individual changes producing a stable frequency of ARTs in the population (Repka & Gross 1995, Gross & Repka 1998, Brockmann 2001). Finally, Shuster & Wade (2003) suggest that current theories of status-dependent selection (e.g. Gross 1996) are limited by their use of the average fitness of males, ignoring the variance between individual males. Whereas the status-dependent selection model suggests that no heritable variation exists for ARTs, Shuster & Wade (2003) argue that genetic polymorphism in male mating behavior may be more common than presently recognized.

15.3 ARTs in male primates

As in other taxa (Henson & Warner 1997), ARTs arise in male primates as a consequence of "winner-take-all" situations, in which reproductive success is skewed to a few dominant males in a population, who employ "bourgeois" mate acquisition tactics (Taborsky 1994,

1997). The resulting reproductive skew favors the evolution of any alternative, "parasitic" behavior that allows inferior quality males to obtain at least some reproductive success, while avoiding the risks of attempting to gain high rank (Taborsky 1994, 1997). The degree of reproductive skew in male primates is determined by the monopolizability of females, which in turn is determined by their spatial distribution, the degree of synchrony of female receptive periods, and the absolute number of females in group-living species (Mitani *et al.* 1996a, 1996b, Nunn 1999, Kappeler 2000a). Most primates live in bisexual groups, where male dominance rank reflects relative power in excluding other males from resources, including oestrous females (van Noordwijk & van Schaik 2003). Skewed reproductive success may also occur where females are dispersed, if dominant males are able to defend home ranges that encompass those of several females to the exclusion of rival males. Reproductive skew may also occur under less obvious circumstances. For example, extra-pair fertilizations (EPFs) are known to occur in pair-living primates (Fietz *et al.* 2000), meaning that some males may be able to increase their relative reproductive success at the expense of other males. However, currently available paternity data are insufficient to determine whether skew occurs in such situations.

Competing primate males have evolved a variety of ARTs by which to overcome the monopolization of females by primary access males. These can be divided into premating, mating, and postmating ARTs (Taborsky 1999, 2001). Premating ARTs are concerned with obtaining access to mates, mating ARTs concern actual mating behavior, and postmating ARTs are concerned with the degree of male investment in parental care. In this section I describe the different ARTs known for male primates, then use Taborsky's (1998) three levels of assessment (determination, plasticity, and selection) to examine the evolution and maintenance of these ARTs in primate populations.

15.3.1 Premating ARTs in male primates

Male primates can increase their likelihood of future mating access to receptive females in various ways, depending on the strategies of females and of other males and on their degree of engagement in male-male competition. In a dispersed social system, males may opt to defend a territory or to be nomadic. In group-living species, males live with a group, alone, or in an all-male band. Possibilities for ARTs thus include dispersal, transfer, and group residency decisions, as well as the tactics used to obtain a group of females (in a one-male, multifemale social system), attract females, and increase the number of females available for fertilization. Finally, male behavioral strategies may be accompanied by morphological differences: while dominant males show maximal development of secondary sexual characters, subordinates males may suppress the development of such characters, reducing intermale competition and investment in reproduction and facilitating the use of behavioral ARTs.

15.3.1.1.Territorial versus nomadic males

The best-studied example of territorial vs. nomadic male ARTs in primates occurs in orang-utans (Box 15.1). A similar situation appears to occur in some galagos and pottos where dominant, territorial "A" males have full adult body weight, and subordinate "B" or vagabond males occupy peripheral ranges (Table 15.1). In these cases, the strategy employed by a male is likely to be dependent on age and condition, and nomadic or "B" males may be younger males waiting for the opportunity to establish a territory (Dixson 1998). Little is known about the reproductive payoffs of the different tactics, although larger male *Galago moholi* have higher mating success than smaller males (Pullen *et al.* 2000).

15.3.1.2 Group membership versus incursions

In group-living species, a prime adult male can achieve high reproductive success as a residential male in a bisexual group, particularly if he is top-ranking (Ohsawa et al. 1993, Borries 2000, Takahashi 2001). However, young or postprime males with lower competitive ability have lower reproductive success as a group-associated male and may increase their reproductive success by living alone or in an all-male group and visiting one or more groups during the mating season to mate opportunistically (Japanese macaques, mandrills, samango monkeys, Hanuman langurs, Table 15.1). Bourgeois, resident males appear to have a reproductive advantage over intruders, but parasitic extra-group males avoid the costs of dominance and have been shown to sire offspring (Berard et al. 1993, Launhardt *et al.* 2001, Keane *et al.* 1997, Soltis *et al.* 2001). A similar situation occurs in some one-male, multifemale species, where all-male bands enter a bisexual group during the annual mating season and mate with females (blue monkeys, red-tail monkeys, and patas monkeys, Table 15.1).

The success of intruder male tactics will depend on the ability of top-ranking group males to exclude newcomers, thereby reducing their likelihood of gaining access to fertile females. Thus multimale influxes in blue monkeys are more likely where there are more oestrous females available and when there are many days with multiple oestrous females available (Cords 2000). The reaction of females to mating attempts from intruding males is also likely to play a role in male reproductive success.

15.3.1.3 Dispersal decisions

In many group-living, nonhuman primate species, males leave their natal group whereas females remain (Pusey & Packer 1987). Male dispersal decisions begin with whether to disperse or to remain in the natal group, and the tactics employed depend on social conditions

and demography. Alternative dispersal decisions are not strictly ARTs, but they heavily influence the availability of mating partners and thus lead directly to ARTs. For example, mature male Thomas' langurs either remain in their natal group as subordinate males, forming an age-graded group (Eisenberg *et al.* 1972), or disperse as juveniles and join an all-male band. Remaining males do not obtain any reproductive success and have not been observed to eventually take over their natal group. However, they increase the length of their father's tenure thereby increasing their own inclusive fitness. They also gain in experience and delay joining an all-male band, where costs are higher than life in a bisexual group (Steenbeek *et al.* 2000b). Male tactics depend on social conditions: age-graded groups develop where male tenure is long enough for male infants to mature in their father's group. However, if a takeover occurs, the new resident male expels any juvenile males (Steenbeek *et al.* 2000b).

Further examples of alternative male dispersal decisions include Costa Rican squirrel monkeys, red howler monkeys, mountain gorillas, and callitrichids (Table 15.1). Male Costa Rican squirrel monkeys either remain in their natal group to breed or disperse and cooperate with age-mates to invade another established group and expel the resident males. The latter strategy occurs more rarely and appears to represent the "best of a bad job", where males are forced out of their natal group due to intrasexual competition (Boinski & Mitchell 1994). Male red howler monkeys either remain in their natal group and aid their father in interactions with extra-group males or disperse. Here male tactics depend on the likelihood of successfully taking over another group, which in turn depends on mean group size and population density (Pope 1990, 1998). In mountain gorillas, the majority of maturing males remain in their natal group, while approximately one third (36%) emigrate (Robbins 1999). The former tactic appears to be more effective and remaining males also gain indirect fitness benefits by protecting infants born in their natal group. Dispersing males are less successful

and may never gain females. The tactic pursued depends on the within-group sex ratio, the age of the current dominant male, and the breeding queue length, and may also depend on the male's relationship to the current male, as males that remain in their father's group inherit his females (Harcourt & Stewart 1981, Robbins 1995, Watts 2000). Finally, male Callitrichids either stay in their natal group as subordinate "helpers" to wait for an opportunity to breed, disperse to found a new breeding group, or join another established group as either a breeding male or a subordinate. Opportunities for dispersing males are dependent on population demography and density; in a saturated habitat males may do better waiting for an opportunity to breed in their natal group, as dispersing males have high mortality and poor chances of finding breeding opportunities elsewhere (golden lion tamarins, moustached tamarins, saddle-back tamarins, Table 15.1).

15.3.1.4 Transfer decisions

In addition to natal dispersal, males of multi-male, multi-female group-living species may subsequently transfer from group to group (secondary transfer, Pusey & Packer 1987). For example, adult male Japanese macaques tend to join troops with few or no males (Suzuki *et al.* 1998), male rhesus macaques transfer to groups with higher male-female ratios (Drickamer & Vessey 1973), and olive baboons and ring-tail lemurs transfer into groups containing more available cycling females (Packer 1979a, Sussman 1992). Males may also transfer between groups briefly during the mating season but return to their long-term group afterwards (rhesus macaques: Lindburg 1969).

The optimal transfer strategy will differ among individual males according to characteristics of the male, such as relative age and competitive ability, status, tenure, and social relationships in the current group, and whether he will leave behind offspring vulnerable to infanticide. The demography of groups available for transfer may also be a

factor, such as the number and relative competitive ability of males and the number of available females (Altmann 2000, van Noordwijk & van Schaik 2003). A male should transfer if the benefits, in terms of improved mating access to females, outweigh the costs, which are made up of the cost of any transition period (e.g. risk of predation and starvation, Alberts & Altmann 1995), and the cost of immigration (e.g. injury risk, Cheney & Seyfarth 1983, Zhao 1996). Determining the long-term reproductive payoffs of male transfer decisions over a male primate's career is not easy, due to the long life span of primates and the difficulty of following the fate of dispersing males (Alberts & Altmann 1995). However, using comparative data, van Noordwijk and van Schaik (2003) have shown that male transfer decisions are strongly affected by the degree of reproductive skew in favor of the top-ranking males in local groups, and that decisions vary predictably with age.

15.3.1.5 Obtaining a harem

In one-male, multi-female group-living species, a male can obtain a group of females in several ways. A male may aggressively take over a breeding group, in a high-risk, high-benefit strategy (geladas, Thomas's langurs, Hanuman langurs, mountain gorillas, red howler monkeys); remain in his natal group or join another group as a subordinate "follower" and wait in a breeding queue (hamadryas baboons) or obtain females by group fission (geladas); or he may acquire females one or two at a time from other groups (mountain gorillas, hamadryas baboons, Thomas' langurs, all references in Table 15.1). The tactics employed by a male will be dependent on many factors but are known to be correlated with population demography and density (Watts 2000). Male reproductive success in one-male, multi-female groups is dependent on tenure length and the size and stability of groups (hamadryas baboons, Colmenares unpubl. data, cited in Watts 2000). In Thomas's langurs, male tactics depend on female group size (groups with more adult females are more likely to

be taken over) and the tenure of group males (females are more likely to leave a long-tenure male) (Steenbeek *et al.* 2000b). In geladas, population growth and increased group size lead to more group fission and thus should lead to more males employing a follower strategy relative to takeover males (Dunbar 1984).

As with transfer decisions, little is known about the relative long-term fitness consequences of these ARTs. However, study of geladas has shown that a male that effects a forceful takeover begins his reproductive career with more females than a "follower" male. A takeover male must wait until he is competitive enough to succeed in male-male competition, and his reproductive career thus begins later than that of a "follower", although they are likely to achieve sexual maturity at the same age. "Followers" have higher chances of success in obtaining females, start reproducing earlier, and have a longer reproductive life, but begin with fewer females. Over a lifetime, these ARTs appear to yield very similar reproductive payoffs (Dunbar & Dunbar 1975, Dunbar 1982, 1984).

15.3.1.6 "Friendships"

Subordinate males may obtain sexual access to at least one female at little risk of aggression from dominant males by forming special relationships, or "friendships", with particular females (Japanese macaques, olive baboons, chacma baboons, rhesus macaques, Table 15.1). Such associations also act to increase female fitness, as male friends protect their infants from infanticidal males (Palombit *et al.* 1997).

15.3.1.7 Alternative morphologies

Although dominant males are generally in their prime, and are therefore likely to be the largest males and in the best physical condition, behavioral ARTs in male primates are not generally paired with dramatic alternative morphologies. However, we have seen that behavioral ARTs in male orang-utans are accompanied by striking differences in appearance

and physiology (Box 15.1). Further examples of morphological differences between males include reduced body mass and condition, reduced testicular volume, decreased levels of circulating testosterone, reduced development of secondary sexual traits, and smaller and less active scent glands in subordinate males (lesser mouse lemurs, moustached tamarins, sifaka, mandrills, Table 15.1). These differences may be due to physiological suppression by the dominant male, or may be mediated by olfactory cues from dominants (Schilling *et al.* 1984, Perret & Schilling 1987a, 1987b) or possibly by visual and/or auditory signals (Maggioncalda *et al.* 1999, Setchell 2003). However, suppression is nonpermanent. For example, even the lowest ranking adult male in a mandrill group can develop the impressive red facial coloration and other secondary sexual traits of dominant males if given the opportunity (Setchell & Dixson 2001b, Fig 15.2).

Suppression of rival males confers a reproductive advantage on the dominant by lessening reproductive competition by reducing sperm competition if suppressed males manage to mate (they have smaller testes), and by reducing their attractiveness to females, if females prefer to mate with males showing full secondary sexual development (orang-utans: Schürmann 1982, Utami 2000, mandrills: Setchell 2002). However, as in "unflanged" male orang-utans (Box 15.1), facultative suppression may also be adaptive in subordinate individuals, by reducing intermale competition and investment in reproduction and facilitating the use of behavioral ARTs (Dixson 1998, Setchell 2003). "Arrested" males thus possess the most adaptive traits for the way in which they seek fertilizations.

15.3.2. Mating ARTs in male primates

The majority of mating ARTs in male primates exist as alternatives to monopolization of females by a dominant male. Such parasitic ARTs include coalition formation and sneak mating and exploit the investment of bourgeois males while avoiding some of the costs of

male-male competition and the constraints imposed by mate-guarding on foraging activity (Packer 1979b, Bercovitch 1983, Alberts *et al.* 1996). Mate choice by both sexes will also influence male mating tactics: males may coerce females that are unwilling to mate.

15.3.2.1 Coalitions

Males in multi-male, multi-female group-living species may form coalitions to force a dominant male to give up a receptive female, leading to mating access to the female (baboons, chimpanzees, Table 15.1), a cooperative behavior similar to that found in reproductive competition in a number of fish species (Taborsky, this volume). Mate guarding by dominant males may become less effective when many males are present (Watts 1998) and the expression of coalitions may also depend on the age structure of males in a group, their tenure, and their social relationships. For example, Alberts *et al.* (2003) conclude that baboon coalitions are more likely when more and older males are present in the group.

15.3.2.2 Surreptitious mating

Low-ranking and extra-group males of many primate species use opportunistic and/or surreptitious mating tactics (chimpanzees, mandrills, baboons, geladas, patas monkeys, rhesus macaques, Japanese macaques, Table 15.1, Fig. 15.3), and sneak copulations that have been shown to result in fertilizations (Ohsawa *et al.* 1993, Berard *et al.* 1994, Manson 1996, Launhardt *et al.* 2001). The opportunity for, and siring success of, sneak copulations will depend on the ability of high-ranking males to monopolize females, and therefore on the number of males and females in a group, the number of extra-group males, and the synchrony of female receptivity.

15.3.2.3 Coercion versus. female choice

Males may use sexual coercion to force females to mate with them against female preference, particularly in species where adult males are larger than adult females (Smuts & Smuts 1993). For example, flanged male orang-utans tend to consort with reproductive females, while unflanged males tend to use force to copulate with females outside consortships (see Box 15.1).

15.3.2.4 Mate selectivity

Males may differ in mate selectivity, depending on their dominance rank. A dominant male that has free choice but is unable to monopolize all available females should concentrate his mating effort on the females who are most likely to conceive and raise his offspring to maturity. Dominant males may thus show less sexual interest in nulliparous females, which are typically less fertile and less adequate mothers than older, experienced females (Altmann 1980), by comparison with females who have already produced at least one infant (baboons, mandrills, Table 15.1). Dominant males may also prefer to mate with high-ranking females (review in Berenstain & Wade 1983), which may be more fertile and able to invest more in resulting offspring (van Noordwijk & van Schaik 1999, Setchell *et al.* 2002). Lower ranking males, on the other hand, for whom choice of mates is limited by male-male competition, should be more likely to mate when the chance arises, even if the chances of fertilization are lower. Thus, while dominant males mate selectively, concentrating their mating attempts when a female is most likely to ovulate, subordinate males mate opportunistically with any female and at times when the female may be less likely to ovulate (rhesus macaques, baboons, chimpanzees, mandrills, Table 15.1).

15.3.3. Postmating ARTs in male primates

Once a new bourgeois male has obtained the position of breeding male in a bisexual group, he may kill the offspring of previous males to increase the number of females available for fertilization because death of an unweaned infants accelerates the resumption of ovarian cycles in females (Hrdy, 1979; see van Schaik & Janson, 2000 for a recent review of evidence for infanticide in primates). Use of this tactic depends on a male's rank and his previous reproductive history within the group. DNA analyses of wild Hanuman langurs have confirmed that male attackers were not related to their infant victims and that presumed killers were the likely sire of subsequent infants (Borries et al., 1999). Further, Palombit et al. (2000) have shown that male chacma baboons express infanticidal behavior facultatively, depending on attributes of the alpha male or conditions of male tenure. The expression of infanticide is also likely to depend on the number of other males in a group, as the presence of other males increases the costs of infanticide, while mating competition decreases the benefits by reducing the ability of the infanticidal male to monopolize subsequent fertilizations (Palombit et al. 2000).

In the majority of primate species males contribute little to the survival of offspring post conception. However, males may protect infants that are likely to be their offspring from other, infanticidal males (long-tail macaques, baboons, Table 15.1). This expression of protective behavior depends on the likelihood of paternity (Buchan et al. 2003).

In an exception to the general primate rule, male callitrichids show extensive infant care (Goldizen 1987, Heymann 2000), and infant survival correlates with the number of adult males present in a group (Garber *et al.* 1984, Koenig 1995). Extreme reproductive skew in females of these species reduces reproductive opportunities for males, which either breed themselves or help raise the offspring of other males (Goldizen 1987). Male tactics depend on social status. Mating and paternity are concentrated in the behaviorally dominant resident male (Baker *et al.* 1993, Nievergelt *et al.* 2000), while subordinates appear to employ a

waiting strategy in the hope of obtaining a breeding position in the future. Subordinates may also gain inclusive fitness, if they are related to the breeding male, but the only genetic study of relatedness available suggests that this is not the case (Nievergelt *et al.* 2000).

15.3.4 Determination, plasticity, and selection of ARTs in male primates

15.3.4.1 Determination

No evidence currently exists for the genetic determination of male ARTs in primates, although it has been suggested that a genetic polymorphism might underlie flange development in orang-utans (van Hooff & Utami, 2004). Environmental modification, however, appears ubiquitous. ARTs are expressed conditionally, although it is possible that genetic variation occurs between individuals in the position of the switch point at which they change from one tactic to another. Male reproductive decisions are dependent on asymmetries in competitive ability, which influence the costs and benefits of each tactic for the individual concerned.

15.3.4.2 Plasticity

Plasticity in male primate ARTs occurs at both the population and the individual level. With the exception of flange development in male orang-utans, which is sequential with a one-time switch point, all reproductive phenotypes appear to be reversible and individuals are capable of changing back and forth between different phenotypes if the opportunity occurs. For example, while former, overthrown harem owners or dominant males are unlikely to attempt to attain top-rank a second time, they will do so if a suitable opportunity occurs, such as a lack of rival males (e.g. mandrills, personal observations). This flexibility is likely to underlie the predominance of behavioral, rather than morphological ARTs, giving males the possibility to facultatively adjust to changing conditions. Reversibility implies hormonal

differences during adult life (Moore 1991), and studies have demonstrated that male ARTs are indeed associated with hormonal differences (e.g. Wickings & Dixson 1992, Maggioncalda *et al.* 1999, 2000, Setchell & Dixson 2001a,b).

15.3.4.3 Selection

The payoff of the monopolization of reproductive females by dominant males, and conversely the success of male ARTs, can be examined by investigating the degree of male reproductive skew. Cowlishaw and Dunbar (1991, 1992) have shown that as group size increases, high-ranking males lose their ability to monopolize access to females, meaning that parasitic male ARTs are more successful. At the population level, Alberts *et al.* (2003) investigated the relationship between male rank and mating success in yellow baboons, using 32 group-years of data. As expected, dominance rank was an important predictor of male mating success--males who spent extended periods at high rank experienced an overall reproductive advantage over males that did not do so. However, parasitic ARTs were more successful when there were many adult males in the group, when group males differed greatly in age, and when the highest ranking male maintained his rank for only short periods.

By their very nature, some male mating tactics (e.g. mate guarding) are easier to observe than others are (e.g. sneak copulations). Thus, although studies of mating success are useful, paternity determination is necessary to truly investigate the impact of ARTs on male reproductive success. In a review of paternity studies in group-living primates, van Noordwijk & van Schaik (2003) have recently shown that an increase in the number of adult males or females in a group is significantly correlated with a decrease in the percentage paternity concentration in the top-ranking male (and therefore a corresponding increase in the success of male parasitic ARTs). As predicted, seasonality of reproduction also had an effect

on the concentration of paternity in the top-ranking male, independent of the number of males (van Noordwijk & van Schaik 2003).

A career perspective (van Noordwijk & van Schaik 2001, 2003) and knowledge of life-history pathways are necessary when considering the costs and benefits of ARTs (Caro & Bateson 1986). For example, we cannot draw conclusions concerning the lifetime success of a male from a one or two year study, when a male's career may last far longer and involve periods of low-, mid-, and high-rank, and accordingly different reproductive tactics and varying payoffs. However, particularly little is known concerning the life-time reproductive success of males following different strategies, or potential associated differences in reproductive lifespan. From the available information, the majority of ARTs in male primates appear to be "best-of-a-bad-job" situations, where lower quality males do the best they can to achieve at least some reproductive success. However, frequency-dependent payoffs to reproductive competitors displaying different ARTs do appear to occur in gelada (Dunbar 1982, 1984) and may also occur in orang-utans (Utami *et al.* 2002).

15.4 ARTs in female primates

In general, far less is known about the sexual strategies of female primates than those of males (Setchell & Kappeler 2003), and attention has generally focused on male ARTs, as in other taxa (Henson & Warner 1997). However, female primates show ARTs at both premating and mating levels, although there is as yet no evidence for postmating ARTs in female primates.

15.4.1 Premating ARTs in female primates

15.4.1.1 Dispersal decisions

Females of most group-living primate species remain in their natal group to breed (Pusey & Packer 1987, Pope 2000). However in some species, females may disperse, giving rise to scope for alternative dispersal decisions based on social conditions and breeding opportunities. For example, female red howlers either remain in their natal group to breed or disperse and form new groups with other dispersing females (Crockett & Pope 1993, Pope 2000). The latter is the most common tactic but is more costly, and many dispersing females die without reproducing. Dispersers suffer more injuries, have a nutrient-deficient diet by comparison to group members, and have delayed age at first breeding (Pope 2000). Dispersal tactics in females of this species depend on the number of resident reproductive females in a group and the presence of the mother. Females always disperse where there are already four or more resident females, and the mother is always present when maturing females remain (Crockett & Pope 1993, Pope 2000). As in males, alternative female dispersal decisions do not represent ARTs per se, but they clearly lead to differences in reproduction between females.

15.4.1.2 Transfer decisions

Females of some primate species may transfer from one group to another during their adult life (Pusey & Packer 1987). Transfer tactics are likely to change with female age and future reproductive potential (Dunbar 1979) and will depend on the social situation. For example, females may emigrate to avoid potentially infanticidal males (Thomas' langurs, mountain gorillas, western lowland gorillas, Table 15.1). Female Thomas' langurs transfer when the current resident male is no longer able to protect offspring from other males, and females are thus more likely to leave a late-tenure male than a short-tenure male (Steenbeek *et al.* 2000a). In mountain gorillas, females prefer to transfer into groups with more than one adult male and fewer females (Watts 2000), in which females enjoy lower risk of infanticide (Robbins 1995,

Watts 2000) and significantly shorter interbirth intervals than in single-male groups (Gerard-Steklis & Steklis 2001). Female western lowland gorilla transfer tactics are also related to social and group demographic factors. In this species, females do not have the option of transferring into multimale groups, which do not occur, but female immigration rates are negatively related to group size and emigration rates are positively related to group size (Stokes et al. 2003).

15.4.1.3 Reproductive suppression

As in males, ARTs can be expected to evolve in females when there is intense intrasexual competition and high reproductive skew. A prime example of such conditions occurs in cooperatively breeding marmosets. High-ranking female marmosets interrupt the copulations of other females, and reproductive function is suppressed in subordinate females (Abbott *et al.* 1990). Suppression is reversible (Abbott *et al.* 1998) and some subordinate females do reproduce in the wild (Nievergelt *et al.* 2000), although any offspring produced are likely to be killed (Digby 1995, Lazaro-Perea *et al.* 2000). Clearly, the best tactic for an adult female is to be dominant, but subordination with reproductive suppression may represent an alternative tactic whereby females avoid wasting reproductive effort while they wait to obtain a breeding position.

Social stress, due to harassment or aggression from high-ranking females, may also act to lower the reproductive success of low-ranking rivals in groups where multiple females breed (Dunbar 1980, 1988). This may represent a tactic by high-ranking females to reduce future competition for nutritional resources from the offspring of subordinates, while low-ranking rivals make the best of a bad job.

15.4.2 Mating ARTs in female primates

Like males, females mate both within consortships and sneakily (Japanese macaques, chimpanzees, mountain gorillas, mandrills, Table 15.1). The mating mode employed depends on the risk of "punishment" by males (sexual coercion); females mate surreptitiously with subordinate or extragroup males, but consort openly with dominant group males. Other possibilities for mating ARTs in female primates include mate choice, competition between females for matings, and the timing of mating behavior. However, it is not yet clear whether discrete differences in reproductive tactics occur between females, and whether these are adaptive.

15.4.2.1 Mate choice

Considerable evidence exists that female primates show mate choice (see Paul 2002 for a recent review). However, while the male chosen may differ between females (e.g. choice for genetic compatibility, Sauermann *et al.* 2001), the rule remains the same (choose the "best" male), thus there are no known mate choice ARTs for female primates.

15.4.2.2 Harassment and avoidance

In one-male, multifemale groups, high-ranking females attempt to prevent low-ranking females from mating through aggression and harassment (patas monkeys, geladas, Hanuman langurs, Table 15.1). This may be because the sperm of the dominant male is limited (Dewsbury 1982, Marson *et al*. 1989, Wedell *et al*. 2002, Preston *et al*. 2003), or because dominant females try to reduce competition of their own offspring with potential offspring of subordinates by preventing the latter from reproducing. Dominant females in multimale, multifemale groups may also aggressively interrupt matings involving subordinate females (rhesus macaques: Loy 1971), and the simple presence of dominant females may inhibit subordinate females from interacting with males (brown capuchins: Janson 1984). These

ARTs are expressed according to social environment: dominant females harass subordinates, while low-ranking females avoid harassment at the cost of reproductive opportunities, a tactic that represents the "best-of-a-bad-job."

15.4.2.3 Timing of mating behavior

Female primates show situation-dependent flexibility in mating behavior that may act to reduce the risk of sexually selected infanticide by nonsire males (Hrdy 1979, Hrdy & Whitten 1987, Smuts & Smuts 1993, van Schaik *et al.* 1999). For example, where group takeover by a new male leads to a high risk of infanticide for infants sired by a previous male, females that are already pregnant solicit the new male for mating ("pseudo-oestrous", Table 15.1), resulting in paternity confusion and reduction in the risk of infanticide.

15.4.3. Postmating ARTs in female primates

Investment in an individual offspring enhances that offspring's chance of survival, while at the same time diminishing a female's ability to invest in future reproduction by reducing her fertility or chances of survival (Fisher 1930, Trivers 1972). Potential postmating ARTs in female primates may therefore include facultative adjustment of investment according to aspects of female condition, such as age, rank, or body condition (Trivers & Willard 1973) or of offspring quality, such as the identity of the sire or the sex of the infant (Qvanstrom & Price 2001). Evidence exists that female primates invest in infant growth and survival according to their own age, growth status, rank, and physical condition (rhesus macaques: Simpson *et al.* 1981, Gomendio 1990, Bercovitch *et al.* 1998; mandrills: Setchell *et al.* 2001, 2002; baboons: Altmann 1980, Johnson 2003; chimpanzees: Pusey *et al.* 1997). Females may also terminate investment in a developing fetus when a newly dominant male is likely to commit infanticide. The benefits from mating with a new dominant male outweigh the costs

of terminating current investment in the offspring of another male (baboons: Pereira 1983; humans: Forbes 1997; Hanuman langurs: Lhota *et al.* 2001). Finally, many studies have examined whether female primates manipulate birth sex ratios according to the social environment or adjust their parental investment according to the sex of an infant. However, these questions have proved difficult to resolve (van Schaik & Hrdy 1991, Hiraiwa-Hasegawa 1993, Silk *et al.* 1993, Brown 2001, Bercovitch 2002, Brown & Silk 2002), and although different sex allocation in offspring would represent alternative allocation phenotypes, it would not represent ARTs. The basic female tactic appears to be the same in all cases: maximize the benefits and minimize the costs of that investment in each offspring in terms of reproductive fitness. Female primates do not appear to employ postmating ARTs, although the possibility exists that they may employ postmating ARTs in terms of fertilization control by physiological mechanisms (cryptic female choice, Eberhard 1985; Eberhard 1996).

15.4.4 Determination, plasticity and selection of ARTs in female primates

As with male primates, all ARTs identified for female primates are influenced by the social conditions in which a female finds herself. Female ARTs are not fixed and are not accompanied by alternative morphotypes. Instead they represent an adaptive response to current conditions and characteristics of the individual female, which determine the relative costs of the tactics. Tactics can thus change if conditions change. The reproductive payoffs are generally unequal, and female ARTs represent the "best-of-a-bad-job" by subordinate females, or females that have fewer resources to invest in reproduction.

15.5 Interactions between male and female strategies

Interactions between the sexes play an important role in the expression and evolution of primate reproductive strategies (Setchell & Kappeler 2003), and of ARTs in general (Henson & Warner 1997). Female reproductive strategies may alter the costs and benefits of male ARTs. For example, males may compete for access to reproductive females, but females can increase reproductive skew among males by showing mate preference for dominant males (orang-utans: Utami 2000, mandrills: Setchell 2002), creating a situation that favors the evolution of male ARTs. Alternatively, female choice for sneak matings with subordinate or extragroup males may act to reduce the dominant male's potential to monopolize females and increase the success of male ARTs (Soltis *et al.* 2001). Male strategies may also limit or determine female strategies. For example, male sexual coercion may prevent females from mating with preferred males, and male infanticide will terminate a female's investment in an infant. Females therefore adjust their mating tactics according to the risk of coercion. The extent to which the strategies of males or females determine the sire of an infant differs with circumstance, and differences may occur between two studies of the same species (Soltis *et al.* 1997a, 1997b, 2001).

15.6 Conclusions

This review allows us to draw some general conclusions concerning primate ARTs. First, a wide diversity of reproductive strategies and ARTs have evolved to promote the reproductive success of individual primates. Underlying this diversity is the bourgeois/parasite paradigm (Taborsky 1994, 1997) and the extent to which individual males are able to monopolize access to mates and the resources available to females for investment in infant growth and survival (Trivers 1972, Emlen & Oring 1977). Perhaps because the effects of male-male competition can be dramatic, intraspecific variation in male mating strategies has received far

more attention than the flexibility of reproductive behavior in female primates. However, females may also employ ARTs, with important implications for lifetime reproductive success.

Second, the types of ARTs employed by the two sexes show both similarities and differences. Premating ARTs in both males and females involve dispersal and transfer decisions, involvement in intrasexual competition, and physiological suppression. However, whereas male-male competition is generally related to access to females, female-female competition is more often related to access to other resources. Both sexes may mate sneakily or with a consort partner, and both may employ mate choice tactics. However, male tactics may involve coercion of females, while females respond to the risk of sexual coercion by manipulating their own mating tactics. Finally, postmating investment tactics are much more important in females, as females are responsible for the majority of parental investment in most primate species, but these do not appear to involve ARTs.

Third, ARTs in primates occur within, as well as between, individuals. They tend to be limited to behavior, gonads, and physiology and are rarely associated with dramatic alternative morphologies. This is likely due to the advantages of plasticity and the lower costs of adjustment according to changes in the characteristics of the individual (age, ontogenetic stage) and in social conditions (e.g. rank).

Fourth, most ARTs in primates appear to be "best-of-a-bad-job" phenotypes, whereby inferior individuals, or those in a suboptimal situation, make the most of any opportunity available to gain reproductive success.

Fifth, in contrast to some other taxa (Henson & Warner 1997, Alonzo *et al.* 2000), and with the exception of female reproductive suppression in common marmosets (Abbott *et al.* 1998), relatively little is known about the life-history pathways underlying ARTs and the factors that determine their expression. This is due to the difficulty of studying long-lived

species, and the fact that primates are not as easy to manipulate experimentally as invertebrates or fish. However, much remains to be learned from the analysis of the entire careers of wild individuals (e.g. van Noordwijk & van Schaik 1999, 2001), allowing us to determine the relative payoffs of alternative tactics, the influence of development on life-time strategies, and how ARTs may change over a lifetime (Setchell & Lee 2003).

Finally, male and female reproductive strategies are intricately linked in primates (van Schaik *et al.* 2003, Setchell & Kappeler 2004), and interactions between the sexes play an important role in the evolution of primate ARTs.

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Fig. 15.1 Flanged male orang-utan (*Pongo abelii*). Unflanged males lack the fatty facial flanges and throat sac, have shorter hair and do not make the characteristic male "long call". Photograph by Benoit Goossens.

Fig. 15.2 Red coloration on the face and genitalia, sternal gland activity, testis size, and testosterone levels in male mandrills before and after gain and loss of alpha status (based on a correlational study). (*) p=0.08, * p=0.05, ** p=0.01 results of paired tests (n=4). From Setchell & Dixson (2001) with permission.

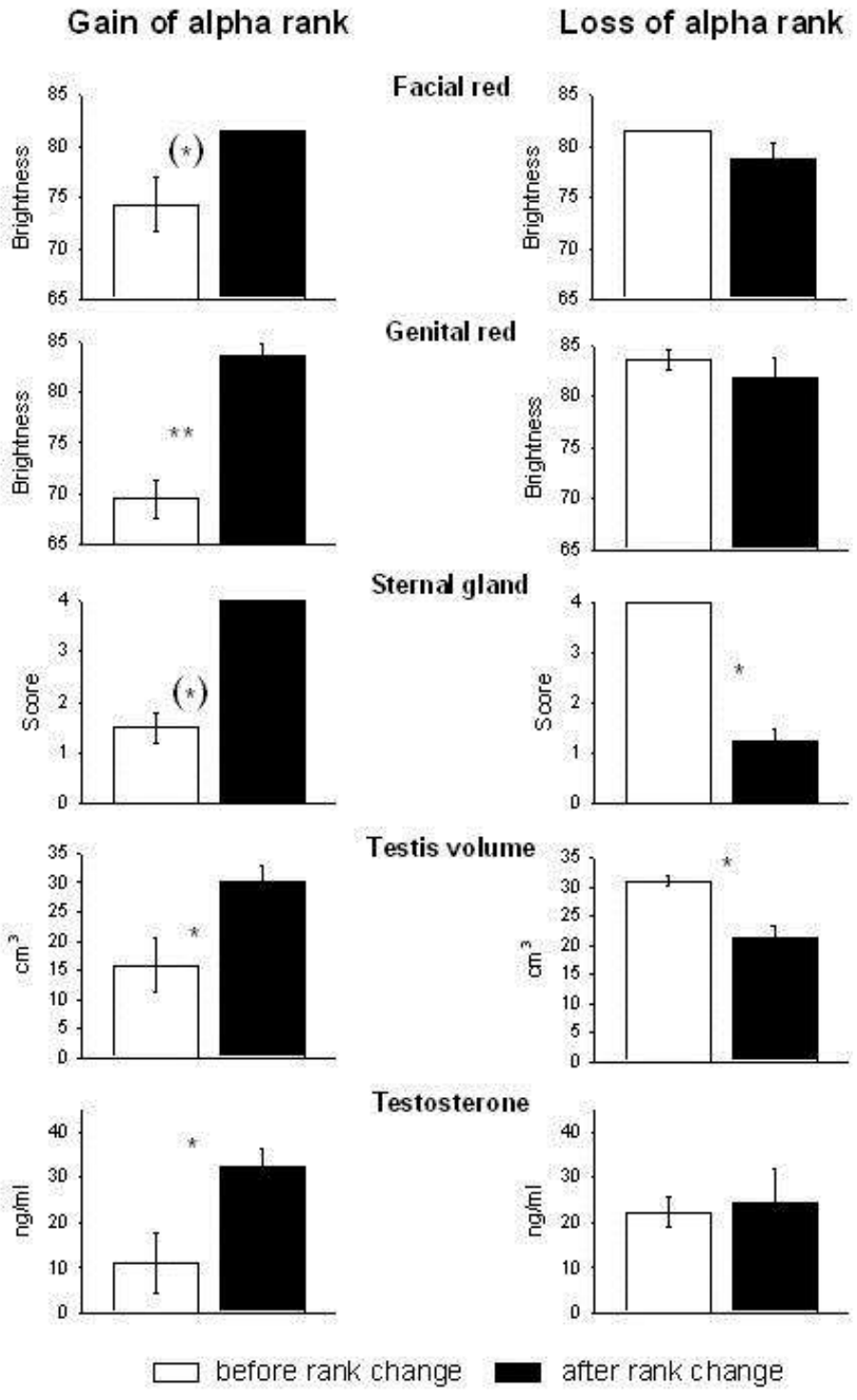
Gain of alpha rank
Loss of alpha rank
Facial red
Genital red
Sternal gland
Testis volume
Testosterone
Brightness
Score
cm³
ng/ml
(*)
**
*
before rank change
after rank change

Fig. 15.3. An adolescent male mandrill (aged 7 years, mass approximately 20kg) mates sneakily with a female showing a large sexual swelling, but who was unlikely to be ovulating at the time of the mating. Males attain adult size (approximately 31 kg) and appearance at 9-10 years, Setchell & Dixson 2002). Photograph of the mandrill colony at the Centre International de Recherches Médicales, Franceville, Gabon, by Joanna M Setchell.

Box 15.1: ARTs in male orang-utans

Orang-utans are semi-solitary, living in over-lapping home ranges in the rain-forests of Sumatra and Borneo (Delgado & van Schaik 2000). Reproductive males may hold a territory, and attempt to monopolise matings with sympatric females (bourgeois males), or they may be nomadic, avoiding contact with territorial males, and mating with females in other males' ranges (parasitic males) (Table 16.1). Territorial males show full secondary sexual development, including fatty facial flanges, long thick hair and a throat sac, and make a characteristic male "long call" (MacKinnon 1974, Fig. 16.1). By contrast, nomadic males do not show flange, hair and throat sac development, and do not make long calls (MacKinnon 1974), although they are sexually mature and fertile (Dixson *et al.* 1982). These two types of males are discrete alternatives, and employ different mating ARTs. Flanged male orang-utans tend to consort with reproductive females, unflanged males tend to use force to copulate with females outside consortships (Galdikas 1981, 1985b, Mitani 1985). However, both flanged and unflanged males have been observed to use both mating tactics (Utami 2000), and the mating tactic employed is likely to depend on the exact situation in which a male finds himself, as well as on individual social relationships.

Development from "unflanged" to "flanged" status can occur at any time after puberty, and males may remain in a state of "arrested development" for more than 20 years in the wild (Utami 2000). Male tactics depend on the social environment: unflanged males are subordinate to flanged males, and develop adult secondary sexual characteristics when dominant males are removed or leave the area (Graham & Nadler 1990, Utami 2000). Endocrine studies in captive orang-utans have shown that arrested males have significantly lower levels of circulating testosterone, dihydrotestosterone (DHT) and luteinising hormone (LH) than adolescent males that are developing adult secondary sexual characteristics (Maggioncalda *et al.* 1999). This suggests that arrested males lack the hormone levels necessary for secondary sexual development, although they have sufficient testicular steroids, LH and FSH to be fertile. Levels of growth hormone are also reduced in arrested males by comparison with developing males, which may explain their smaller body mass (Maggioncalda *et al.* 2000).

Dominant male orang-utans benefit from suppressing development in rival males by reducing male-male competition for access to females. However, facultative suppression of secondary sexual development may also be adaptive in subordinate males, acting to

ameliorate inter-male competition, reduce investment in secondary sexual traits, and facilitate alternative behavioural mating tactics (Dixson 1998, Setchell 2003). Indeed, Utami *et al.* (2002) have shown that both morphs of male sire offspring in the wild, suggesting that unflanged males are successful at obtaining fertilisations, and do not delay reproduction until they are sufficiently dominant to develop full secondary sexual characteristics.